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Published in:
Perspectives in plant ecology evolution and systematics

DOI:
10.1016/j.ppees.2012.12.001

Publication date:
2013

Perspectives in Plant Ecology, Evolution and Systematics 15 (2013) 32–44

Contents lists available at SciVerse ScienceDirect

Perspectives in Plant Ecology, Evolution and Systematics

journal homepage: www.elsevier.com/locate/ppees

Forum

An integrated perspective to explain nitrogen mineralization in grazed ecosystems

Maarten Schrama[a,b,*,1], G.F. (Ciska) Veen[a,b,c,1], E.S. (Liesbeth) Bakker[d], Jasper L. Ruifrok[a], Jan P. Bakker[a], Han Olff[a]

[a] Community and Conservation Ecology, University of Groningen, Nijenborg 7, P.O. Box 11103, 9700CC Groningen, The Netherlands
[b] Department of Terrestrial Ecology, Netherlands Institute of Ecology, P.O. Box 50, 6700 AB Wageningen, The Netherlands
[c] Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, SE901 83 Umeå, Sweden
[d] Department of Aquatic Ecology, Netherlands Institute of Ecology, P.O. Box 50, 6700 AB Wageningen, The Netherlands

ARTICLE INFO

Article history:
Received 25 January 2012
Received in revised form
19 November 2012
Accepted 4 December 2012

Keywords:
Grazing
Trampling
Soil compaction
Soil texture
Soil type
Water logging
Nutrient cycling
Decomposition
Excreta (dung and urine)
Soil aeration

ABSTRACT

Large herbivores are key drivers of nutrient cycling in ecosystems worldwide, and hence they have an important influence on the productivity and species composition in plant communities. Classical theories describe that large herbivores can accelerate or decelerate nitrogen (N) mineralization by altering the quality and quantity of resource input (e.g. dung, urine, plant litter) into the soil food web. However, in many situations the impact of herbivores on N mineralization cannot be explained by changes in resource quality and quantity.

In this paper, we aim to reconcile observations of herbivores on N mineralization that were previously regarded as contradictory. We conceptually integrate alternative pathways via which herbivores can alter N mineralization. We illustrate our new integrated perspective by using herbivore-induced soil compaction and subsequent changes in soil moisture and soil aeration as an example.

We show that the net effect of herbivores on mineralization depends on the balance between herbivore-induced changes in soil physical properties and changes in the quality and quantity of resource input into the soil food web. For example, soil compaction by herbivores can limit oxygen or water availability in wet and dry soils respectively, particularly those with a fine texture. This can result in a reduction in N mineralization regardless of changes in resource quality or quantity. In such systems the plant community will shift towards species that are adapted to waterlogging (anoxia) or drought, respectively. In contrast, soils with intermediate moisture levels are less sensitive to compaction. In these soils, N mineralization rates are primarily associated with changes in resource quality and quantity.

We conclude that our integrated perspective will help us to better understand when herbivores accelerate or decelerate soil nutrient cycling and improve our understanding of the functioning of grazed ecosystems.

Introduction

Large vertebrate herbivores are key determinants of plant community composition, productivity and the functioning of many ecosystems worldwide (Olff and Ritchie, 1998; Knapp et al., 1999; Bardgett and Wardle, 2003; Cromsigt and Kuijper, 2011). One of the major pathways through which large herbivores affect the plant community is via their influence on nutrient cycling and soil nutrient availability (Fig. 1, McNaughton, 1984; Georgiadis et al., 1989; Hobbs, 1996; Frank et al., 2000; Bardgett and Wardle, 2003). Herbivores can either speed up or slow down rates of nitrogen (N) mineralization (Hobbs, 1996; Bardgett and Wardle, 2003). Classical theories that explain the impact of large herbivores on N cycling primarily focus on herbivore-induced changes in the quality and quantity of resources that are returned to the soil food web, i.e. dung, urine and plant litter (Fig. 1; McNaughton, 1984; McNaughton et al., 1997b; Bardgett and Wardle, 2003; Pastor et al., 2006). Herbivores speed up N mineralization through the deposition of dung and urine and by promotion of fast growing species and high quality (palatable) regrowth (with a low C/N-ratio), hence enhancing litter quality. In contrast, they slow down N

* Corresponding author at: Department of Terrestrial Ecology, Netherlands Institute of Ecology, P.O. Box 50, 6700 AB Wageningen, The Netherlands.
Tel.: +31 317473596.
E-mail address: M.Schrama@nioo.knaw.nl (M. Schrama).
[1] These authors contributed equally to the work.

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http://dx.doi.org/10.1016/j.ppees.2012.12.001

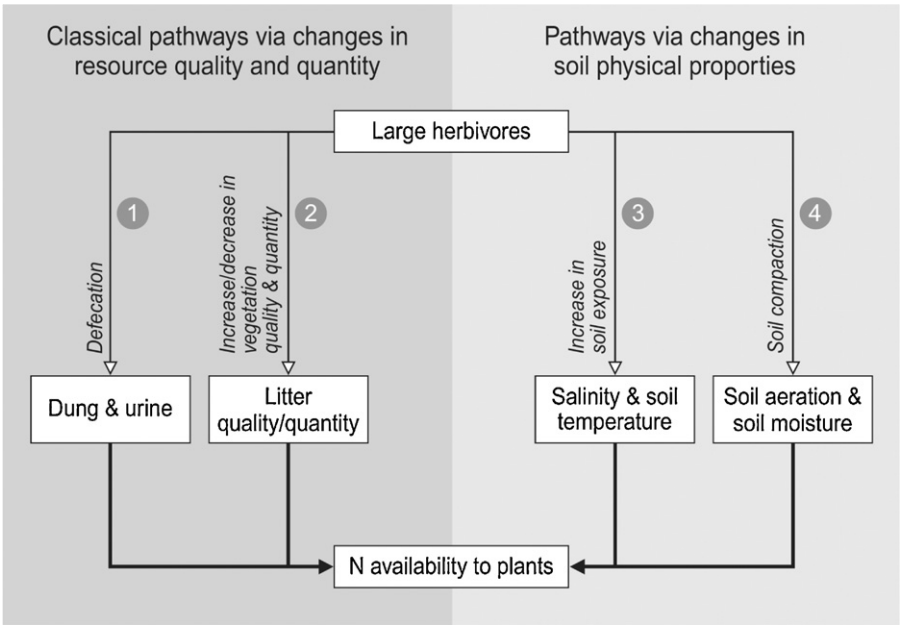

Fig. 1. Overview of the influence of large herbivores on the nitrogen (N) cycle in grasslands. This diagram depicts four main pathways via which herbivores can affect soil N mineralization. Prevailing theories mainly focus on pathways 1 and 2 via which herbivores alter the quality of resources entering the soil food web, i.e. by excreting dung and urine and by changing plant quality and quantity. Pathways 3 and 4 operate through soil physical properties. Pathway 3 describes the effects of herbivores on the exposure of bare soil, thereby increasing soil temperature or soil salinity (e.g. Gornall et al., 2009; Buckeridge and Jefferies, 2007). Pathway 4 represents effect of large herbivore trampling via soil compaction on soil moisture and soil aeration, which consequently affects N mineralization (discussed in this article).

mineralization rates when promoting low-quality plant species (with a high C/N ratio), hence decreasing litter quality (Hobbs, 1996; Ritchie et al., 1998). The acceleration of N mineralization rates through nutrient deposition and stimulation of plant growth is the basis of the grazing optimization hypothesis (McNaughton, 1979) which may apply under a restricted set of conditions (De Mazancourt et al., 1998).

Although changes in the quality of resource input into the soil food web can explain the impact of large herbivores on N cycling in a number of ecosystems (McNaughton, 1984; Pastor et al., 1993; Ritchie et al., 1998; Wardle et al., 2002; Harrison and Bardgett, 2004; Persson et al., 2005), they cannot explain contrasting effects of large herbivores on N mineralization in many other situations (e.g. Biondini et al., 1998; van Wijnen et al., 1999; Kiehl et al., 2001; Bakker et al., 2004; Su et al., 2004; Pei et al., 2008; Wang et al., 2010; Shan et al., 2011; Gass and Binkley, 2011). For example, in some systems plant quality increased under grazing, but mineralization rates were reduced (Chaneton and Lavado, 1996; van Wijnen et al., 1999; Kiehl et al., 2001). Even in a large-scale comparison across different sites herbivore effects on soil N cycling could not be understood from changes in plant quality (Bakker et al., 2006, 2009). Therefore, there is a need to explore additional mechanisms that can explain herbivore-induced changes in N cycling (Gass and Binkley, 2011).

In the current theories on large herbivores and N mineralization (McNaughton et al., 1997a; Bardgett and Wardle, 2003), impacts that run via soil physical conditions received little attention (Gass and Binkley, 2011). However, large herbivores can be major drivers of changes in soil physical conditions, for example, of soil moisture and oxygen contents and soil temperature (Fig. 2). This can in turn have important consequences for N mineralization rates (Hamza and Anderson, 2005). Therefore, in this paper we explore whether integrating herbivore-induced changes in soil physical conditions into current theories on N cycling in grazed systems will help us to understand when herbivores speed up or slow down N mineralization. We aim to reconcile contrasting observations into a novel perspective, to be able to understand the impact of herbivores on N mineralization across a wide range of ecosystems.

We start by proposing the key drivers of soil N mineralization, i.e. resource quality and quantity and soil physical conditions, that should be integrated into theories on N mineralization in grazed ecosystems. Then we use trampling-induced soil compaction as an example to illustrate in detail how herbivores can alter N mineralization via changing soil physical conditions and how an integrated perspective can help us to understand the impact of herbivores on N

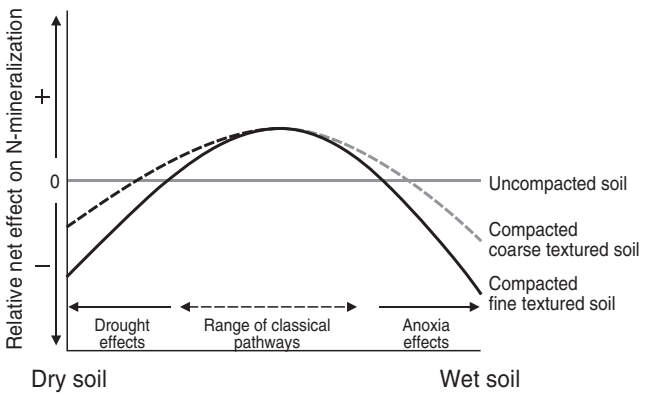

Fig. 2. Hypothetical changes in N mineralization as a result of herbivore trampling in soils with different textures. All effects are scaled relative to an uncompacted soil (dotted straight line). On a relatively fine-textured soil (clay: solid line) herbivore compaction may lead to soil anoxia (wet end of the gradient) and strongly reduced water infiltration (dry end of the gradient), both affecting net N mineralization negatively. These effects may outweigh the positive effects on N mineralization via litter quality and quantity. At intermediate moisture availability, effects that operate via increased plant quality, plant quantity, dung and urine) result in a positive effect of large herbivores on N mineralization. On a relatively coarse textured soil (sand: striped line), herbivore trampling induced effects on N mineralization are less pronounced, and may therefore be outweighed by effects through excreta, litter quantity and quality. Grey part of striped line indicates the range in which no studies were found.

mineralization across a range of ecosystems. Finally, we will discuss the implications of the integrated perspective for plant communities and we indicate directions for future research.

Herbivore effects on N mineralization

The net soil N mineralization rate is defined as the rate at which mineral forms of N (ammonium and nitrate) become available for uptake by plants through a complex of biological decomposition and transformation processes (Swift et al., 1979; Chapin et al., 2002). Mineral N is mainly released in the form of ammonium through decomposition of plant litter by soil organisms. Ammonium can be transformed into nitrate. Mineral N is used by soil microbes and plants, and it can be lost from a system through leaching, volatilization and denitrification. The rate at which soil organisms mineralize N is primarily determined by the quality of the plant litter that enters the soil food web (Parton et al., 2007; Cornwell et al., 2008). High quality litter is decomposed faster (Cornelissen, 1996). In addition, soil physical conditions, such as temperature, moisture and aeration can be major drivers of the activity of soil organisms and therefore are important determinants of mineralization (Hamza and Anderson, 2005; Powers et al., 2005; Bardgett and Wardle, 2010) and denitrification (Laanbroek, 1990). Hence, the rate at which organic forms of N are transformed into inorganic forms is affected by two key drivers, i.e. the quality and quantity of resources for the soil food web and the soil physical conditions. Large herbivores can strongly modify both resource quality and quantity (Bardgett and Wardle, 2003; Pastor et al., 2006), as well as soil physical conditions (Asner et al., 2004; Gass and Binkley, 2011).

Resource quality and quantity

The classical studies on herbivores and N cycling focus on herbivore-induced changes in the quality and quantity of resources (e.g. plant litter and dung and urine) that enter the soil food web. These theories advocate that herbivores can speed up soil N cycling through the deposition of dung and urine, which provide easily available nutrients and stimulate the activity of soil microbes (Frank and McNaughton, 1993; McNaughton et al., 1997b; Frank and Groffman, 1998; Augustine et al., 2003). Moreover, herbivores can increase the allocation of nutrients to roots and they may stimulate root exudation in plants (Holland and Detling, 1990), which may favour soil microbial activity (Hamilton and Frank, 2001). Accelerated N cycling enhances plant N uptake and leaf N concentrations (e.g. Holland and Detling, 1990; Hamilton and Frank, 2001) and increases the quality of plant litter. This can result in a positive feedback loop (McNaughton, 1984; McNaughton et al., 1997a) where herbivores enhance soil N availability, and in turn increase plant litter quality and thus rates of soil mineralization (Cornwell et al., 2008). In high-fertility ecosystems, herbivores may further accelerate N cycling by favouring the proportion of fast-growing, palatable plant species in a community (Augustine and McNaughton, 1998; Cromsigt and Kuijper, 2011).

Negative effects of herbivores on N cycling are mainly explained by a decrease in the proportion of palatable plant species in a community (Pastor et al., 1993; Hobbs, 1996; Ritchie et al., 1998; Knops et al., 2000). Especially in ecosystems with low soil fertility, where the overall plant quality is low, herbivores selectively feed on high-quality subordinate species (such as legumes vs. grasses in grasslands, or deciduous tree saplings vs. conifers in forests). This can result in a shift in community composition towards less palatable species with lower litter quality and decelerated decomposition rates, hence leading to a lower N mineralization (Ritchie et al., 1998; Augustine and McNaughton, 1998; Knops et al., 2000; Wardle et al., 2002; Harrison and Bardgett, 2004; Persson et al., 2005; Pastor et al., 2006).

Soil physical conditions

The other major pathway via which herbivores can alter soil N mineralization rates encompasses herbivore effects on soil physical conditions. Herbivores can alter the soil physical conditions via different mechanisms (Fig. 1). First, herbivores can increase the exposure of bare soil by removing the aboveground vegetation, which changes the temperature and moisture regime in the soil. This may speed up mineralization in ecosystems where soil temperature is limiting the activity of soil organisms, because soil temperature can increase due to reduced insulating capacities of the vegetation (Olofsson et al., 2004; Gornall et al., 2007, 2009). Alternatively, removal of vegetation may strongly increase evaporation at the soil surface, resulting in higher salinity and reduced N mineralization (Srivastava and Jefferies, 1996; Buckeridge and Jefferies, 2007), although reduced vegetation cover may also result in less water loss through transpiration (Zhang and Schilling, 2006).

Second, a key factor through which large herbivores alter soil physical conditions is trampling (Bilotta et al., 2007). Trampling can compact the soil, which will affect many different abiotic soil characteristics such as pore size, soil moisture and soil aeration. Compaction-induced changes in these soil characteristics have been indicated as major drivers of altered N mineralization rates, because they strongly affect the activity of the soil organisms (Hamza and Anderson, 2005; Powers et al., 2005; Drewry et al., 2008). Reduced pore size in a compacted soil increases the water holding capacity. This is positive for N mineralization when water is limiting N mineralization (Stanford and Epstein, 1974). However, this is negative when it results in water saturation and oxygen limitation, which is generally above 30% soil moisture (Sierra, 1997; Paul et al., 2003; Drewry et al., 2008). Moreover, when small pore sizes limit water infiltration in dry soils, compaction can also have a negative influence on mineralization rates. Additionally, low air filled porosity as a result of soil compaction can result in high denitrification, which can result in a significant loss of inorganic N via gaseous emissions (Haunz et al., 1992; Lipiec and Stepniewski, 1995). Moreover, small pores restrict the body size of soil fauna and physically protect many food sources for soil organisms, which also contributes to a reduction in N mineralization (Verhoef and Brussaard, 1990; Breland and Hansen, 1996; Bouwman and Arts, 2000; Berg et al., 2001; Osler and Sommerkorn, 2007; Sorensen et al., 2009).

The magnitude of compaction is determined by the soil texture, because relatively fine-textured soils (soils with >10% clay) are more sensitive to compaction than relatively coarse-textured soils (soils with <10% clay), because the fraction of small pores becomes much larger in a fine-textured soil (Van der Linden et al., 1989; Rasiah and Kay, 1998). Consequently, whether the effect of herbivore-induced soil compaction on N mineralization is positive or negative may vary along a gradient of soil moisture and soil texture (Fig. 2; Rasiah and Kay, 1998; Hamza and Anderson, 2005). We did not take organic soils (>20% organic matter) into account.

Integrated perspective

Large herbivores can strongly modify both key drivers of N mineralization, i.e. resource quality and quantity (Bardgett and Wardle, 2003; Pastor et al., 2006), as well as soil physical conditions (Asner et al., 2004; Bilotta et al., 2007; Gass and Binkley, 2011). Therefore, we propose that integrating the modification of soil physical properties by herbivores with the longer acknowledged effects on

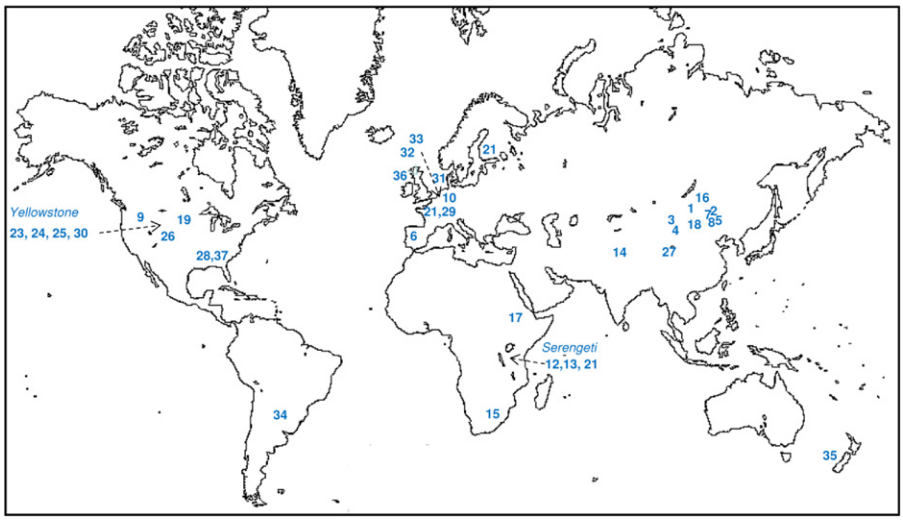

Fig. 3. World map with the locations of the studies that were used in this article.

the quality and quantity of resource input will advance our understanding of N mineralization in grazed ecosystems. The net effect of herbivores on mineralization will depend on the balance between herbivore-induced changes in soil physical properties and changes in the quality and quantity of resource input into the soil food web. In some systems, the impact of herbivores on soil physical conditions may be modest. In such systems herbivore-induced changes in N mineralization will primarily depend on changes in the input of dung and urine or on changes in the quality and quantity of plant litter. Hence, classical theories will explain the impact of grazing on N cycling in these systems (Ritchie et al., 1998; Augustine and McNaughton, 2006; Pastor et al., 2006). In contrast, in many other systems herbivores may have a very strong impact on soil physical conditions. If these effects outbalance the impact of herbivores via classical pathways, the impact of herbivores on soil physical conditions may explain the net effect on N mineralization. In such situations, differences in plant quality do not necessarily reflect differences in N mineralization rates (Biondini et al., 1998; van Wijnen et al., 1999; Kiehl et al., 2001; Bakker et al., 2004; Su et al., 2004; Xu et al., 2007; Zhang et al., 2008; Pei et al., 2008). Considering soil physical conditions may thus help us to reconcile observations of herbivores on N mineralization that were regarded as contradictory to classical theories on N cycling.

Application of our integrated perspective: does it increase our understanding?

We use herbivore-induced soil compaction and subsequent changes in soil moisture content as an example to examine whether our integrative perspective improves our understanding of herbivore effects on N cycling.

We hypothesize that the importance of compaction-induced changes in soil physical conditions varies across ecosystems. We expect that the magnitude of compaction effects varies along a gradient of soil moisture and soil texture (Fig. 2). In compactable, wet or dry soils the impact of herbivores on N mineralization will be mediated by changes in soil water availability, thereby outbalancing the classical resource pathway. In contrast, in soils that are less compactable or with intermediate moisture content the resource-mediated pathway will be dominant in driving herbivore effects on N mineralization.

We explored the literature of herbivore impact on N mineralization rates to test our hypothesis qualitatively and quantitatively.

Literature search

We searched for empirical studies that investigate how herbivores affect N mineralization. We found 165 studies on N mineralization in grazed systems in Thomson Reuters ISI Web of Science using the keywords "herbivores" OR "grazers" AND "mineralization". From this search we included 37 studies in our literature review (Fig. 3), based on the following criteria. Studies had to report in situ measurements of N mineralization in the presence of large herbivores and under ungrazed conditions, either as year-round measurements or from the wet/growing season. We only used studies performed under (semi-) natural conditions and excluded highly overgrazed agricultural systems. The studies had to include information on soil moisture content and/or soil texture, since these are key factors driving the magnitude of compaction effects (Rasiah and Kay, 1998). Organic soils (OM content > 20%) were not included in this study.

We grouped studies according to soil texture (relatively fine texture: >10% clay; relatively coarse texture: <10% clay) and soil moisture content in ungrazed soil (very dry soil: <10% gravimetric water content; intermediate: 10–30% gravimetric water content and high: >30% gravimetric water content), to be able to evaluate how the impact of compaction varies across different ecosystems. Below 10% and above 30%, soil moisture content becomes unfavourable for N mineralization (Stanford and Epstein, 1974; Paul et al., 2003; Wang et al., 2010), because at very low soil moisture water becomes limiting and at very high soil moisture soils become water-logged and oxygen becomes limiting for soil organisms. In the studies that we collected, soil texture and soil moisture were measured in the upper soil layer (0–15 cm). When there was no information on the percentage of clay in the soil, we used the description of the soil type to determine whether a soil was fine- or coarse-textured. For example, fine-textured soils were described in the literature as loam, loamy clay, silty loam, glacial till, dark chestnut or sandy loam. Coarse-textured soils were described as cambisol, dystric cambisol, sandy soil, loamy sand, sandy dunes, clay sand or coarse texture. We collected the N concentration in plants as a proxy for plant quality to test whether grazing-induced changes in N mineralization were related to changes in plant quality, or to changes in soil abiotic conditions.

Finally, we also collected data on other environmental properties that can be drivers of N mineralization rates such as soil temperature, soil acidity, and soil organic matter content (Hassink

Table 1
Reported effects of herbivore grazing on N mineralization, soil moisture and vegetation quality, categorized by texture and soil moisture.

	Reference	Ecosystem	Herbivore density	Grazing excluded (number of years)	Effect on N mineralization	Moisture class (low: <10%; medium: 10–30%; high: >30%)	Moisture content (%)	Effect on soil moisture	Effect of grazing on vegetation quality	Clay content (%)	Organic matter content (%)	pH	Annual precipitation (mm, along-year average)	Average temperature (°C, along-year average)
Relatively coarse textured soils (% clay < 10%)														
1	Su et al. (2004)	Steppe	na	5	–	LOW	9	–	na	3	1–5%	7–8.2	366	6.5
2	Xu et al. (2008)	Steppe	Moderate (1.3 sheep ha^{-1})	17	–	LOW	5.5	–	na	9	2–6%	na	350	−0.4
3	Pei et al. (2008)	Steppe	High (1 sheep ha^{-1})	6	–	LOW	2.5	–	–	2	1–2.5%	8.7–8.9	134	9
4	Liu et al. (2011)	Steppe	Low-high (0–9 sheep ha^{-1})	9	+/–	LOW	4.5	–	0	7	5.7–5.9	8.4–8.6	359	7.1
5	Shan et al. (2011)	Steppe	Low-high (0–9 sheep ha^{-1})	4	––	LOW	10	–	+	2	2.7–4.1%	6.9–7.5	346	0.3
6	Peco et al. (2006)	Open woodland	0.5 cow ha^{-1}	30	+	LOW	11.5	na	+	9	1–3%	na	550	na
7	Xu et al. (2007)	Steppe	na	17	–	LOW	7.5	–	na	9	1–2%	6.7–6.9	350	−0.4
8	Zhang et al. (2008)	Steppe	na	4	–	LOW	8	–	na	na	1–3%	6.9–7.2	385	2.1
9	Rexroad et al. (2007)	Steppe	Low (<1 animal 100 ha)	35	0	LOW	4.5	–	–	na	na	na	224	10.7
10	Bakker et al. (2004)	Temp. grassland	1 cow ha^{-1}	10	–	MEDIUM	25	na	+	na	9–10%	4.2	770	9.2
11	Kooijman and Smit (2001)	Dune grassland	na	4	–	MEDIUM	na	na	–	2	na	na	825	10.1
12	Augustine et al. (2006)	Savanna	na	1.4	+	MEDIUM	na	na	na	10	na	na	516	na
13	McNaughton et al. (1997a)	Savanna	Low (natural densities)	na	++	MEDIUM	na	na	na	na	na	na	1009	na
14	Bagchi and Ritchie (2010)	Steppe	Low (<1 animal 100 ha^{-1})	2.5	+	MEDIUM	na	na	na	na	na	7.7–7.9	283	na
15	Coetsee et al. (2011)	Savanna	na	na	+	MEDIUM	na	na	+	na	na	na	na	na
	Rexroad et al. (2007)	Steppe	Low (<1 animal 100 ha^{-1})	55	+	MEDIUM	14	na	+	na	na	na	250	10
Relatively fine textured soils (% clay > 10%)														
16	Giese et al. (2011)	Steppe	High (1 sheep ha^{-1})	28	0	LOW	11	–	+/–	15	na	na	348	−0.3
17	Tessema et al. (2011)	Open woodland	na	na	–	LOW	na	na	0	na	3–4	6.4–6.7	512	26
	Tessema et al. (2011)	Open woodland	na	na	–	LOW	na	na	+	na	1.6–1.8	8.0–8.1	512	26
18	Wang et al. (2010)	Steppe	na	5–25	–	LOW	10	na	+	24	2–3	7.1–7.3	350	0.4
19	Biondini et al. (1998)	Steppe	Medium (50% biom. remov.)	5	–	LOW	na	––	+	35	4–5	na	455	4
	Peco et al. (2006)	Open woodland	0.5 cow ha^{-1}	30	+	MEDIUM	19	na	+	18	3–4	na	550	na
20	Augustine et al. (2003)	Savanna	Low (0.3 wild animal ha^{-1})	na	+/–	MEDIUM	na	na	na	12	na	na	na	na
21	Mikola et al. (2009)	Temp. grassland	High (max. sustain. yield)	3	0	MEDIUM	20	0	+	20	3–5.9	6.2	298[b]	Na

Table 1 (*Continued*)

	Reference	Ecosystem	Herbivore density	Grazing excluded (number of years)	Effect on N mineralization	Moisture class (low: <10%; medium: 10–30%; high: >30%)	Moisture content (%)	Effect on soil moisture	Effect of grazing on vegetation quality	Clay content (%)	Organic matter content (%)	pH	Annual precipitation (mm, along-year average)	Average temperature (°C, along-year average)
22	Le Roux et al. (2003)	Temp. grassland	na	13	+	MEDIUM	na	na	na	26	na	na	770	8
23	Frank et al. (2000)	Temp. grassland	0.3 animal ha^{-1}	38	+	MEDIUM	28	na	+	24	1–16	7.2–7.3	361	4.5
	Frank et al. (2000)	Temp. grassland	0.3 animal ha^{-1}	38	+	MEDIUM	na	na	+	Na	na	7.6–7.7	361	4.5
24	Patra et al. (2005)	Temp. grassland	na	13	+	MEDIUM	na	na	na	na	3–5	5.5–5.7	770	8
25	Tracy and Frank (1998)	Temp. grassland	na	36	0/+	MEDIUM	23	na	+	23	1.0–4.3	6.3–7.7	752	1.1
26	Gao et al. (2008)	Alpine meadow	na	na	+	MEDIUM	na	na	na	na	3–6	na	na	na
27	Wang et al. (2006)	Subtrop. grassl.	na	3	0	MEDIUM	14	na	na	na	10.8–12.2	4–6.2	na	na
28	Rossignol et al. (2006)	Temp. grassland	1 cow ha^{-1}	10	+	MEDIUM	na	na	+	na	na	na	na	na
29	Frank (2008)	Temp. grassland	na	36	0	MEDIUM	11.9	+	+	na	1–4.3	6.3–7.7	na	na
30	Kiehl et al. (2001)	Salt marsh	Low-high (0–10 sheep ha^{-1})	5	−−	HIGH	40	–	+	30	3–4	na	700	na
	Kiehl et al. (2001)	Salt marsh	Low-high 0–10 sheep ha^{-1})	5	–	HIGH	36	–	+	30	3–4	na	700	8.9
31	Schrama et al. (2012)	Salt marsh	0.5 cow ha^{-1}	38	−−	HIGH	40	0	+	40	7–7.3	na	680	9.2
32	van Wijnen et al. (1999)	Salt marsh	Low (0.5 wild animal ha^{-1})	5	−−	HIGH	40	+	+	40	na	na	680	9.2
	van Wijnen et al. (1999)	Salt marsh	0.5 cow ha^{-1}	10	–	HIGH	50	+	+	40	8–14	na	680	9.2
33	Chaneton and Lavado (1996)	Pampa	Med.–high (0.5–1 cow ha^{-1})	13	–	HIGH	31	+	na	23	3.0–3.1	na	900	na
34	Gass and Binkley (2011)	Alpine meadow	Low (<0.1 moose ha^{-1})	16	0/–	HIGH	39.5	na	na	na	7–8	>7	350	4
35	Menneer et al. (2005)	Temp. grassland	No–medium–high	na	+[a]	HIGH	na	+	na	na	6.8	5.4	na	na
	Tracy and Frank (1998)	Temp. grassland	na	36	0/+	HIGH	40	na	+	27			752	15
36	Olsen et al. (2011)	Salt marsh	Low (0.2 cow ha^{-1})	40	–	HIGH	48	+	+	na	12–14	7.4	na	na
37	Wang et al. (2006)	Subtrop. grassl.	na	3	0/–	HIGH	35	0/+	+	na	10.5–15.5	4–6.2	na	na
	Frank (2008)	Temp. grassland	na	36	0	HIGH	35.8	+	+	30	15.7	7.8–7.9	368	4.5

Per study, duration of the experiment, organic matter content of the soil, soil pH, herbivore density and the ecosystem type are indicated. Scores of herbivore effects were assigned as reported in the papers. References without a number are mentioned multiple times. Effects of herbivore grazing on N mineralization were categorized as follows: '−−': >50% decrease; '−': 0–50% decrease; '0': no significant effect; '+': 0–50% increase; '++': >50% increase. Effect on vegetation quality can be negative ('−': higher C/N-ratio in response to grazing) and positive ('+': lower C/N-ratio in response to grazing) in the same study, in that case this was indicated with '+/−'. Herbivore density was noted according to the wording of the different papers. na: not available.

[a] Single experimental trampling event in an agricultural pasture.

[b] Rainfall only measured during growing season (June-July).

et al., 1993; Sierra, 1997; Frank, 2008), herbivore types, grazing intensity, length of grazing experiment (Owen-Smith, 1992; Cumming and Cumming, 2003) and average annual rainfall and temperature (Table 1).

We first explored our hypotheses with a qualitative review of the studies that we found in our literature search. We then analyzed the impact of soil texture (i.e. fraction of clay) and soil moisture content on the change in mineralization rate in grazed sites with a regression model. In this analysis we only used the studies that presented actual values for soil moisture and soil texture. In this set of studies, soil moisture and texture were highly confounded. Most studies were either carried out on dry, coarse-textured soils or on wet, fine-textured soils. Therefore, in our current analysis we could not fully separate the impact of soil moisture and soil texture. Moreover, the estimates of soil moisture reflect a very rough measure (usually only measured a few times during the growing season at the same time when N mineralization samples were collected). Because it fluctuates strongly in most soils, our analysis may underestimate the strength of this correlation (as given in Kiehl et al., 2001). In addition, we also tested whether other factors, such as pH, organic matter content and grazing history, influenced changes in N mineralization.

N mineralization rates, soil moisture, soil texture and plant quality and quantity

Wet soils

Seven studies carried out on wet, fine-textured soils report a reduction in N mineralization under grazing by large herbivores (Table 1; e.g. Lavado and Alconada, 1994; van Wijnen et al., 1999; Kiehl et al., 2001; Schrama et al., 2012). In such soils, compaction may increase the amount of water-filled pores to such an extent that oxygen becomes limiting for aerobic decomposition and N mineralization (Lipiec and Stepniewski, 1995; Startsev and McNabb, 2007). All studies carried out on wet, fine-textured soils indeed report an increase in water-filled porosity in the presence of herbivores, presumably as a result of trampling (Table 1). Subsequently, reduced oxygen availability may cause an increase in denitrification (Menneer et al., 2005; Olsen et al., 2011), because nitrate will be used as the first alternative electron acceptor when oxygen is not present, resulting in a loss of mineral N (Wollersheim et al., 1987; Laanbroek, 1990).

We found one exception where mineralization peaks under wet conditions in an agricultural pasture that was experimentally trampled (Menneer et al., 2005). However, this may reflect a short-term response to trampling which could be explained by a sudden input of litter into the soil. N mineralization rates on the long term may have been affected very differently, but were not measured in this study.

Grazing-induced changes in N mineralization rates on wet soils did not concur with changes in plant quality. All studies on wet soils reported a reduction in N mineralization by grazing, plant quality was enhanced or was not affected in these studies (Table 1). Legumes were reported to be absent (Chaneton and Lavado, 1996; van Wijnen, 1999; Kiehl et al., 2001). Hence, in grazed, wet soils it appears that plant quality is not an important driver of N mineralization. In contrast, we can understand reduced N mineralization under grazing in wet systems from the increase in soil water availability and the related reduction in soil oxygen availability. Therefore, we propose that in these systems herbivore-induced changes in water availability may outbalance classical pathways via altered resource quality. An example from a long-term grazed (23 years), temperate salt-marsh (van Wijnen, 1999) illustrates this principle on a wet, fine-textured soil (Fig. 4). During a full growing season (March–October), N mineralization rates were measured in three treatments: a grazed, a hand mown treatment (to remove vegetation, but avoid compaction), and an ungrazed treatment. According to classical theories, the observed increase in vegetation quality and abundance of dung and urine in the grazed treatment (Bakker, 1989) would have been expected to lead to an increase in N mineralization. Nonetheless, a strong reduction in N mineralization was observed in the grazed treatment (Fig. 4a), which was accompanied by an increase in soil moisture and bulk density (Fig. 4c and e) (and probably an even stronger increase in water filled porosity). Moreover, even though the (non-compacting) mowing treatment had a similarly positive effect on vegetation quality as the grazed treatment (Bakker, 1989), N mineralization was threefold higher than in the grazed treatment and not significantly different from the ungrazed treatment (Fig. 4a). These findings support the idea that grazer-induced soil compaction caused the observed differences in N mineralization, not the quality of the resource input into the soil.

We did not find any study on the impact of large herbivores on N mineralization on coarse-textured, wet soils. Probably this situation is very exceptional, since coarse-textured soils generally have a low water holding capacity as a result of the large pore size and therefore are usually relatively dry. If there are wet, coarse-textured soils, we would speculate that herbivores can still reduce N mineralization, because they may limit the oxygen diffusion similarly to fine-textured soils. However, since coarse-textured soils are much less sensitive to compaction, the effects may be less strong than on fine-textured soils.

Dry soils

All five studies on dry, fine-textured soils report that large herbivores reduce N mineralization rates (Table 1). In these soils, moisture decreases in response to grazing (Table 1; Pei et al., 2008; Wang et al., 2010; Giese et al., 2011; Tessema et al., 2011) due to reduced water infiltration through trampling in combination with increased evaporation at the soil surface (Allington and Valone, 2010; Jeddi and Chaieb, 2010). Under such conditions water content becomes limiting for N mineralization (Sierra, 1997; Wang et al., 2010).

Moreover, under dry conditions, the combination of reduced water infiltration and high evaporation at the soil surface may result in high concentration of for instance chloride, sodium, calcium or boron (Lavado and Alconada, 1994; Chaneton and Lavado, 1996). Increased levels of salinity as a result of herbivore trampling may impose an additional constraint on N mineralization (Lavado and Alconada, 1994; Chaneton and Lavado, 1996; Srivastava and Jefferies, 1996).

In contrast to N mineralization, plant quality was generally enhanced under grazing in dry, fine-textured soils. While in more moist systems the increase in resource quality often results in a higher rate of N mineralization (McNaughton et al., 1997a), apparently in these dry soils a higher vegetation quality does not lead to a higher N mineralization. This implies that there are other grazing-induced factors that limit N mineralization. Consequently, in analogy to wet soils, herbivore-induced changes in soil physical conditions may outbalance changes in plant quality in dry, fine-textured soils. A long term (25 years) grazed steppe (Wang et al., 2010) illustrates this principle on a dry fine-textured soil (Fig. 4). Also here, vegetation quality increased, but N mineralization decreased (Wang et al., 2010). This decrease in N mineralization was accompanied by significantly lower soil moisture, thus suggesting that herbivore induced soil compaction resulted in limited mineralization in these soils via a reduction of soil moisture. Additionally, removal of aboveground biomass may have resulted a more bare soil, thus leading to higher transpiration and lower soil moisture.

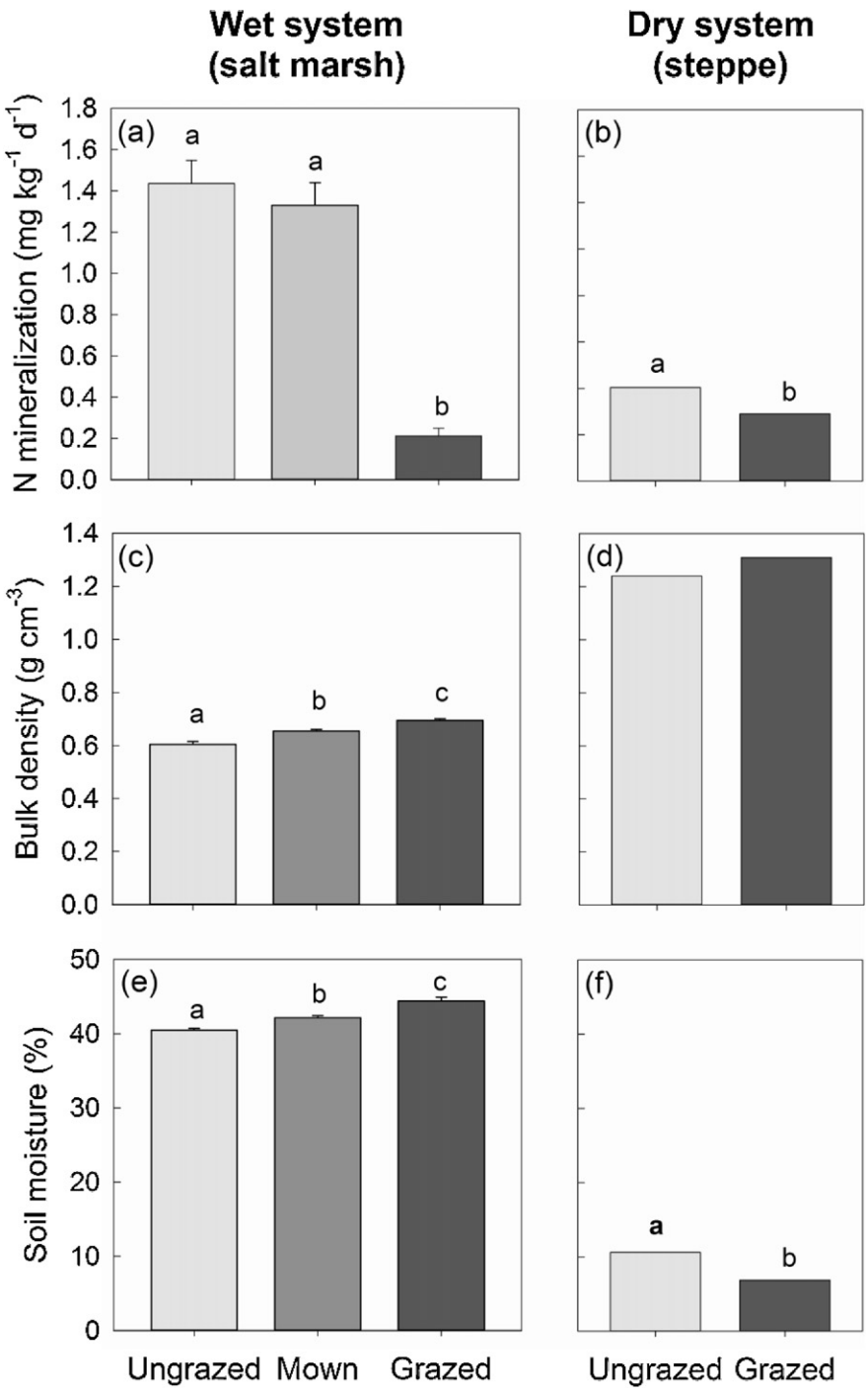

Fig. 4. Changes in N mineralization, bulk density and soil moisture content in a very wet soil (grazed salt marsh) and a very dry soil (grazed steppe). Data for the wet system were collected on a temperate salt marsh on the back-barrier island of Schiermonnikoog in the Netherlands (53°30′N, 6°10′E) (van Wijnen, 1999), with a relatively long growing season (data collected between 20 March and 19 October 1995). In this study, daily N mineralization rates, bulk density and soil moisture were measured in situ in plots that were ungrazed (excluded from grazing for 22 years), hand-mown (aboveground biomass was removed once a year for 22 years, but plots were not trampled), or cattle-grazed (stocking density 0.5 cow ha^{-1}). Average soil moisture content on the salt marsh is higher than 40% with a clay-silt content of more than 40%. Data for the dry system originate from a study in a dry temperate steppe in northern China (116°42′N, 43°38′E) with a shorter growing season (data collected between 11 May and late September (Wang et al., 2010)). In this study N mineralization rates, bulk density and soil moisture were measured in situ in plots that were ungrazed (excluded from grazing for 25 years) and plots that were grazed as a normal local practice by for example, sheep, camels and yak. Average soil moisture in these soils was lower than 10% with a clay-silt content around 25%. Data are means ± SE. Error bars for (b), (d) and (e) are not presented due to lack of data. No significances are presented in (d) (bulk density), due to lack of data. Different letters indicate significant differences ($\alpha = 0.05$).

In dry, coarse-textured soils, six out of nine studies show a negative effect of herbivore grazing on soil moisture content and N mineralization (Table 1), probably also operating via reduced infiltration and enhanced evaporation. For example, Shan et al. (2011) showed a reduction in N mineralization and soil moisture in a dry steppe system, while plant quality increased. This indicates that herbivore-induced changes in soil physical conditions in these soils may also outbalance changes in resource quality. However, there

are also studies showing that herbivores can increase both soil N mineralization and plant quality in dry, coarse-textured soils (e.g. Peco et al., 2006). Moreover, in a number of studies, it is difficult to disentangle the impact of herbivores on N mineralization via changes in soil moisture content and via changes in vegetation quality, because soil moisture, plant quality and N mineralization were all reduced under grazing (Rexroad et al., 2007; Pei et al., 2008). Consequently, on coarse-textured soil, both classical effects of herbivores through altering resource quality (e.g. Peco et al., 2006) or herbivore-induced changes in soil physical conditions (e.g. Shan et al., 2011) may play a role in driving N mineralization. From our literature study we cannot predict which pathway is important under which conditions in dry, coarse textured soils. This may depend on other environmental properties such as grazer identity and density that may become important determinants of N mineralization.

Intermediate soil moisture content

Thirteen out of 20 studies carried out in soils with intermediate soil moisture report an increase in N mineralization in response to grazing. In six of these studies, plant quality was measured, and in all cases plant quality increased in the grazed treatment (e.g. Frank et al., 2000; Augustine and McNaughton, 2006; Table 1). Studies on soils with intermediate soil moisture content that report a negative effect of herbivores on N mineralization also report a reduction in plant quality (Ritchie et al., 1998; Kooijman and Smit, 2001; Wardle et al., 2002; Pastor et al., 2006). Therefore, on soils with intermediate soil moisture content the link between plant quality and N mineralization rates holds, both in fine- and coarse-textured soils (Pastor et al., 1993; McNaughton et al., 1997a; Ritchie et al., 1998; Singer and Schoenecker, 2003). Apparently, in such soils neither soil oxygen availability, nor soil moisture availability seems to be a dominant factor limiting N mineralization. As a result, changes in resource quality and quantity probably outbalance the pathway via changes in soil physical conditions under intermediate moisture conditions. However, very few studies in the intermediate soil moisture range actually quantified soil physical conditions. Hence, we cannot determine the relevance of the pathway operating via soil physical conditions.

Relationships between soil moisture, texture and changes in N mineralization

We found a strong unimodal relationship between the soil texture (clay fraction) and the effect of grazers on N mineralization (Fig. 5a, 2nd order polynomial regression, $R^2 = 0.40$, $P < 0.001$). Both on coarse- and on fine-textured soils, grazers have a negative effect on net N mineralization. Moreover, we found a unimodal relationship between soil moisture and the effect of grazers on N mineralization (Fig. 5b, $R^2 = 0.17$, $P < 0.05$). At both very low and very high soil moisture, grazers have a negative effect on N mineralization, while under intermediate moisture levels grazers have a positive effect on N mineralization. These analyses show that grazers have the most important (negative) effect on N mineralization in dry, coarse-textured conditions and wet, fine-textured conditions. This confirms the hypothesis in Fig. 2. However, we could not test whether the impact of grazing on N mineralization was stronger on fine-textured soils than on coarse-textured soils, since soil moisture and soil texture were highly confounded (Fig. 2). Therefore, the regression analysis provides a first indication that soil moisture and texture may be important drivers of the impact of large herbivores on N mineralization in terrestrial systems. Moreover, it confirms that our proposed framework may help us to better understand N mineralization in grazed ecosystems. To further understand the impact across environmental gradients it will be necessary to carry out controlled grazing experiments along gradients of soil moisture and soil texture (see for example Schrama et al., 2012).

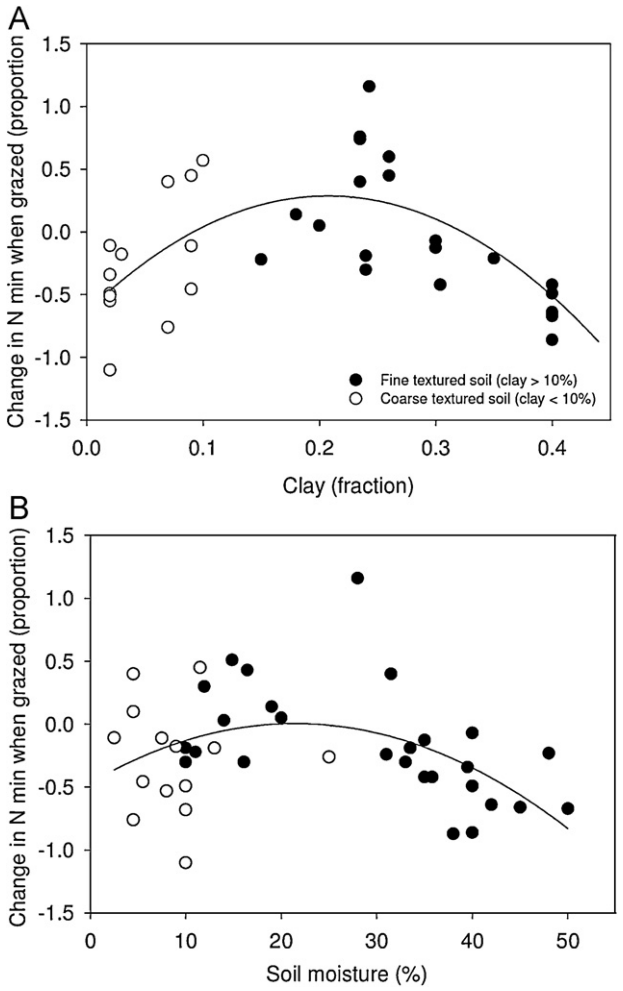

Fig. 5. Proportional change in N mineralization as a result of grazing, as predicted by soil clay content (a) and initial soil moisture content (b). The symbols depict data from the studies given in Table 1. Proportional change is calculated as following: (ungrazed N_{min} − grazed N_{min})/ungrazed N_{min}. Open symbols depict coarse-textured soils (clay < 10%), closed symbols depict relatively fine-textured soils (clay > 10%). The lines result from a second order polynomial regression (a): $R^2 = 0.40$, $P < 0.001$; (b): $R^2 = 0.17$, $P < 0.05$.

In our analysis we found unimodal relationships between soil characterisitics and N mineralization, indicating that at intermediate soil moisture and soil texture herbivores generally speed up mineralization rates. However, in the literature overview we showed that this is not always the case. In some ecosystems herbivores can reduce mineralization rates at intermediate moisture and texture when they reduce plant quality (e.g. Pastor et al., 1993; Ritchie, 1998; Pastor and Durkee Walker, 2006). Most of these studies were not included in our regression analysis because they did not report the appropriate soil parameters.

None of the other (abiotic) variables (climate, pH, organic matter content, and grazing history) shows any relationship with the effect of grazers on the change in N-mineralization (Electronic appendix, Fig. 1). Although, locally variation in these factors may drive the impact of large herbivores on N mineralization rates, they appear to be less important to explain large-scale patterns.

N mineralization and plant communities

Generally, rates of N cycling are strongly linked to the quality of the plants and plant litter (Wardle et al., 2004). As described in the classical theories on N cycling in grazed ecosystems, large herbivores can strengthen this positive feedback. This leads to enhanced N mineralization when herbivores increase plant quality (McNaughton et al., 1997a), and to a reduction in N mineralization when they decrease plant quality (Pastor et al., 1993; Ritchie, 1998; Kooijman and Smit, 2001; Wardle et al., 2002), for instance when legumes become less abundant due to grazing (Knops et al., 2000). However, in systems where herbivore-effects on N cycling via soil physical properties are very important, such as in systems on the wet and dry end of the soil moisture gradient, the intimate link between N mineralization and the quality of the plant community may become decoupled by herbivore grazing. With our literature review, we showed that the impact of herbivores on N mineralization via soil physical conditions may outbalance effects via litter quality and quantity. In turn, these changes in soil physical conditions may become the main factor driving changes in plant quality and plant species composition. On the dry end of the moisture gradient, grazers can reduce soil moisture levels, which could result in selection for drought tolerant plant species, such as a shift towards higher abundances of C4-grasses (Epstein et al., 1997). In studies where grazing results in such a shift in plant species composition, this can lead to either lower or higher vegetation quality (Milchunas and Lauenroth, 1993; Biondini et al., 1998; Adler et al., 2004; Zhang et al., 2008; Shan et al., 2011), often irrespective of changes in N mineralization (Biondini et al., 1998; Shan et al., 2011). On soils with high clay content, such effects can be expected to be even larger as physiological drought (the actual availability of water to plants) is larger on a fine textured soil (Anderson et al., 2007).

Likewise, on the wet end of the moisture gradient, large herbivores can increase soil moisture, thereby selecting for plant species tolerant to waterlogging, such as species that possess specific root traits (e.g. the formation of aerenchyma or radial oxygen loss) that allow them to cope with reduced oxygen availability in the soil (Justin and Armstrong, 1987; Colmer, 2003). Plant species that increase in grazed plant communities on compacted, waterlogged soils are often of higher quality than the plant species that are dominant on wet soils under ungrazed conditions (Bakker, 1989; Chaneton and Lavado, 1996; Kiehl et al., 2001; Garibaldi et al., 2007) even though N mineralization in these communities is reduced (Chaneton and Lavado, 1996; van Wijnen, 1999; Kiehl et al., 2001). So, while a close link between the quality of the vegetation community and the rate of N mineralization has often been assumed, we suggest that these links may be less strong on both ends of the soil moisture gradient. However, in order to advance our understanding of herbivore grazing on plant community characteristics along a moisture gradient, these ideas need further testing.

Other factors influencing N mineralization

We showed that in systems where quality and N cycling are decoupled, grazing-induced changes in soil moisture and soil texture can explain the impact of grazing on N cycling relatively well. Nonetheless, herbivores can also influence N mineralization via other abiotic pathways, for example by changing soil temperature, soil pH, P content, lateral water transport and soil organic matter content (Hassink et al., 1993; Mwendera and Saleem, 1997; Curtin et al., 1998; Cornelissen et al., 2007; Frank, 2008), as well as the spatial rearrangement of nutrients (Frank et al., 2000; Bakker et al., 2004), and leaching and ammonia volatilization (Ruess and McNaughton, 1988). Moreover, variability and seasonality in rainfall can also be important drivers of changes in N mineralization. For example, when a system becomes wetter after rainfall, the impact of herbivores will shift along the moisture axis in Fig. 2. In a dry period, herbivores may reduce N mineralization in a dry year by reducing water availability to decomposing microbes, while in a wetter herbivores may speed up N mineralization by increasing water holding capacity in the soil.

In addition, also herbivore density (Biondini et al., 1998; Kiehl et al., 2001) and herbivore type may affect the strength and direction of herbivores on N mineralization. For example, studies reported that N mineralization may be optimal at low (Biondini et al., 1998; Kiehl et al., 2001), intermediate (Shariff et al., 1994; McNaughton et al., 1997a) or high (Barger et al., 2004; Gao et al., 2008) grazing intensity. Only studies on coarse-textured soils did not find any effects of herbivore density (Xu et al., 2007; Shan et al., 2011).

Since many factors may alter rates of N mineralization in natural ecosystems, we perceive our integrated perspective as a first step in a research agenda that opens new avenues for a more general, conceptual understanding of herbivore effects on N cycling.

The way forward

We showed that using our integrated perspective may advance the understanding of the effect of herbivores on N mineralization. However, there is little experimental evidence to support our novel perspective on herbivores and N mineralization (but see Schrama et al., 2012). There is a need for field experiments that explicitly test the relation between net N mineralization and soil compaction, soil texture and soil moisture and potentially other abiotic variables. In this context, water-filled porosity, rather than gravimetric soil moisture, should be measured, because the first is much more indicative of moisture-related processes that could hamper N mineralization. As grazing-induced changes in plant quality, vegetation composition and effects on N mineralization may play out over long time-scales, these field experiments should be performed over a considerable time period as well, probably on the scale of decades (e.g. van Wijnen et al., 1999; Pei et al., 2008; Wang et al., 2010; Shan et al., 2011). One recent study by Schrama et al. (2012) investigated how cattle affected soil compaction, soil moisture and N mineralization across coarse- and fine-textured soils in a moist, natural grassland in the Netherlands. They showed that large herbivores decrease N mineralization on clay soils through compaction and increased soil moisture content, while on sandy soils herbivores had little effect on soil moisture, soil compaction and N mineralization. This study provides the first experimental evidence that contrasting effects of herbivores on N mineralization can be explained by changes in soil abiotic properties.

Conclusion

In this paper we reconciled the effects of herbivores on N mineralization, by explicitly integrating herbivore-induced changes in plant quality with the impact of herbivores on soil physical properties. We used herbivore effects on soil moisture as an example to evaluate whether soil physical conditions can increase our understanding of N mineralization in grazed ecosystems worldwide. In very wet and dry systems, particularly with a fine soil texture, effects of herbivores on N mineralization can be understood from changes in soil moisture content, but not from changes in plant quality. In contrast, in systems with intermediate soil moisture content, particularly those with a coarse texture, herbivore-induced changes in plant and hence litter quality are intimately linked to changes in N mineralization. Therefore, our integrated perspective

can help us to better understand herbivore-induced changes in N mineralization across a range of terrestrial ecosystems.

Acknowledgements

We thank Theo Elzenga, Wim van der Putten, Matty Berg for helpful comments on previous versions of this review. We are also grateful to the four anonymous reviewers and the handling editor for their comments and suggestions, which greatly improved the quality of this article. We thank Harm van Wijnen for sharing his data. This is Publication 5389 of the Netherlands Institute of Ecology (NIOO-KNAW).

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ppees.2012.12.001.

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